ALTITUDINAL EFFECTS ON THE GENERAL DIVERSITY OF ENDEMIC INSECT COMMUNITIES IN A LEEWARD HAWAIIAN FOREST SYSTEM MANUKA FOREST RESERVE, SOUTH KONA, HAWAI'I

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INTRODUCTION

The amazing diversity of form and habitat in the Hawaiian native insect fauna is currently an object of review and study. Perhaps 4000 species of endemic insects have been described, and new species are often encountered in general collections of remoter areas. Thus, a pioneering stage still prevails in Hawaiian forest entomology.

Many species of introduced insects (especially those of economic importance) have been well studied, and aspects of their taxonomy, physiology, behavior, and ecology are relatively well known. In contrast, many of the Hawaiian insects are so poorly understood that all the information available may be a type specimen and general collection information. Some species holotypes are defined from as little as wing fragments from a single specimen, never again re-encountered (Zimmerman 1948).

One of the recent trends in Hawaiian entomology is the utilization of transect techniques along altitudinal gradients. These studies have demonstrated that species are often restricted to well-defined altitudinal ranges (Gagné 1976). There are usually habitat limitations related to altitude which define optimal ranges and distribution boundaries.

This study examines the distribution of endemic insect families along an altitudinal gradient between 1670 and 580 m, and investigates differences in the diversity of the families at various elevations. The trends uncovered would provide insight to environmental and biotic factors related to altitude, affecting the distribution of the Hawaiian insect fauna.

STUDY SITE

The ahupua'a of Manuka, Kaulanamauna, and Kapu'a lie upon the southwestern flank of the Mauna Loa shield volcano in the South Kona district of the island of Hawai'i. These triangular sections of land extend downslope from their common apex at Pu'u Ohohia (1690 m) along the Southwest Rift Zone of Mauna Loa, fanning outward to include a 12 km expanse of shoreline at their bases (USGS topographic quadrangles 1967).

METHODS

Transects and sample stations

Field study was conducted from June 15 to July 31, 1977. The survey of insect fauna was one aspect of a holistic ecosystem baseline survey of the Manuka area conducted under the auspices of the National Science Foundation.

Twelve sampling stations were established along two parallel transect access lines in altitudinal increments of 290 m running from Pu'u Ohohia downslope. The arrangement of sampling stations is illustrated in Figure 1. This placement established two replicate stations at the 1440, 1150, and 875 m elevations, and one replicate at the 585 m elevation. The study area boundaries precluded establishing replicates at the 1690 m level, while commercial agriculture at one of the 585 m plotsites made considerations of sampling at that location moot.

Whenever possible, the entomology sampling station plotsites coincided with that of the Manuka Research Project vegetation ecology survey sites, in order to have available detailed vegetation data.

Sampling techniques

In this study, only the night fauna was considered. Night collection commenced at 7:00 PM and ran continuously to 10:00 PM. Each night collection utilized a simple sheet light trap. A Coleman-type lantern provided attractive illumination. All insects that came to rest upon the sheet were collected during the 3-hour period, and kept for identification. Large insects were collected with sweep nets, while smaller insects were aspirated into vials.

Data analysis

The number of families encountered at each plot were cumulated, and mean values for isoaltitudinal plots were computed. The trends in the diversity of insect communities at the family

level were analysed against altitude distributions of the sample station plotsites via correlation coefficients generated by:

$$r = \frac{s_{xy}}{s_x s_y} \text{ where } s_{xy} \text{ (covariance)} = \frac{1}{n-1}\left(\Sigma x_i y_i - \frac{1}{n}\Sigma x_i \Sigma y_i\right)$$

$$\text{and } s_x = \sqrt{\frac{\Sigma x_i^2 - (\Sigma x_i)^2/n}{n-1}} \qquad s_y = \sqrt{\frac{\Sigma y_i^2 - (\Sigma y_i)^2/n}{n-1}}$$

where s_x and s_y are standard deviations, x and y being values of two discrete and changing factors: altitude and the number of insect families encountered.

RESULTS

There was a general linear increase in the number of families collected with decreasing altitude (Table 1). Correlation coefficients calculated using the mean number of families collected at isoaltitudinal plots substantiated this linear relationship ($r = -0.72$, $n = 5$).

With decreasing altitude, greater numbers of families appeared during the first half of the collection periods. At the 1690 m station, 50% of families encountered were collected by the midpoint of the collection period. At 1150 m, this figure had increased to 70%, while at 875 m it was 79% and at 585 m, the insects collected by the first half of the collecting period amounted to 84% of the total yield. The rise in this temporal packing correlated with altitude ($r = -0.74$, $n = 12$).

An interesting exception to the linear relationship of both family diversity and temporal packing trends ocurred at the 1440 m elevation, where both diversity and packing exceeded figures characteristic of the 1150 m plots, and were only slightly lower than values at the 875 m level. This "hump" is easily seen in Figure 2. If the data from the 1440 m plots are deleted, and correlation coefficients are again calculated, the linear fit against altitude is far more precise (family diversity/altitude $r = -0.82$, $n = 9$; temporal packing/altitude $r = -0.91$, $n = 9$).

The distribution of entomology sites, vegetation ecology relevé stations, habitat descriptions, and climatic observations along the altitudinal gradient are presented in Figure 3. The number of vascular plant species and insect families encountered at identical sites are compared in Figure 4. The data is utilized in the discussion to assess vegetational correlations and to incorporate several situations to interpret both general trends and the "hump" phenomenon.

DISCUSSION

The trend of increasing diversity in insect communities with lower altitude that was uncovered in the study area was expected by this author. Major dimensions critical to the survival and fitness of insect species, such as temperature and moisture, approached more favorable conditions with decreasing altitude. In addition to these environmental aspects, the effect of vegetational diversity can be considered.

Environmental Aspects

Temperature

On the even, lee slope of the Mauna Loa shield volcano, mean temperature decreases with altitude. It is not unusual to find morning frost at the 2000 m level, while at sea level, nights are often uncomfortably warm. There is some evidence that temperature effects contributed to limiting the upper range of many insect species in this study. The total number of specimens per collection increased with decreasing altitude, and the numbers of insect families which appeared by the first half of the collection period increased from five families (50% of the total families collected) at 1690 m, to 18 families (84% of the total families collected) at 585 m. Clearly, not only were there more insect families encountered, but more total specimens collected, and a much greater relative activity at lower elevations. The difference in activity was especially notable. At 1690 m, less than 100 specimens were collected, and long periods of inactivity were prevalent by the end of the collection period, when night temperature was estimated at 5°C. In contrast, at the 585 m plotsites, several hundred specimens were collected, and near the end of the collecting period, the collectors were hard-pressed to keep up with the insects clustered on the sheet and swarming around the light. The estimated temperature at the end of the night collection there was 15°C.

Beetles in the family Scolytidae were not encountered except below 875 m, where they were quite common. Scolytid beetles are known in *Metrosideros* wood, and *Metrosideros* sp. exists as the dominant macrophanerophytic species in the entire study area. Thus, food limitations cannot be imposed. Increasing moisture conditions toward 1150 m is not a limiting factor. Scolytids are known from rain forests as well as mesophytic forests. Predation is a factor to consider; however, bird species such as *Loxops* and *Himatione* exist at both low and higher altitudes, and the incidence of predacious and parasitic insects increases with lower altitude. It seems likely that temperature is the limiting factor. Little is known of the temperature tolerances of the Hawaiian insects, and because no systematic temperature readings were taken in this study, no conclusions can yet be made.

Moisture

The climatic pattern along the Kona Coast of the island of Hawai'i is clearly defined from the predominant tradewind situation in the Hawaiian Islands. Due to the massive obstacle of the Mauna Loa shield volcano which negates tradewind influences, the Kona (leeward) flank climate is determined largely by a diurnal convective cycle.

In the day, land heat-induced winds pull moisture-laden ocean air up the slope of Mauna Loa. An inversion layer near 1100 m induces cloud formation in a band above this level, where highest precipitation occurs. Above and below this level, average rainfall decreases along gradients (Blumenstock & Price 1967). From the barren cinder above 1700 m, moisture levels increase downslope toward fog forest at 1440 m, and mixed mesophytic forest below this to approximately 300 m, where near-xeric conditions prevail. Within the altitude range of the study, however, moisture conditions are seen to increase downslope. If moisture is considered as a limiting factor, then the good agreement between moisture gradients and insect family diversity leads to the conclusion that the increase in moisture and the increase in insect diversity are related.

In a study of the distribution of canopy-associated arthropods along a transect on the windward slope of Mauna Loa, Gagné (1976) suggested that factors contributing to the distribution of the more restricted arthropods would appear to be related to climate. For example, in his study, the exotic detritivorous roach, Allacta similis, was apparently excluded from higher montane environments, a phenomenon which Gagné attributed to cooler temperature and greater moisture in the lower rain forest (below 1800 m). In the same manner, he noted that the detritivorous tree cricket, Paratrigonidium spp., predominated in moister, warmer sites at the lower portions of the transect (below 1500 m). In a more general trend, Gagné found that arthropod species diversity in Acacia koa tree canopies was relatively high at low and mid-elevations, but decreased markedly with altitude, which he attributed to climatic causes.

In the Manuka study, moisture conditions were considerably different from the Mauna Loa findings, where tradewind influences push the inversion layer higher, and mesic conditions prevail to about 200 m, with rain forest environments restricted to below 1400 m. In the Manuka study area, rain forest environment does not exist, and mesic conditions exist in a band of precipitation largely below 1400 m and above 400 m. We would expect that the upper altitudinal limit, if it is determined by relative humidity, would be lower than those observed along the Mauna Loa transect.

In the day collections at Manuka, Allacta similis was not found above 1150 m plotsites. In nocturnal collections, the crickets, Paratrigonidium spp., likewise were limited to below 1150 m. A rarer, brachypterous ground cricket, Leptogryllus sp., was found only at 860 m, despite concerted searches of leaf

litter habitats at lower and higher altitudes. Although both Paratrigonidium and Leptogryllus are poorly scleroterized, Leptogryllus is an especially soft-bodied insect. The tendency toward hot, xeric conditions at lower elevations, and the tendency toward colder, xeric conditions at higher elevations seem to have restricted the range of this fragile, wingless, detritivorous cricket.

Desiccation pressure and the alleviation of this factor at lower altitudes seems likely to play a role in determining the increase of diversity seen in the study area. However, until determinations can be made about the optimum moisture conditions for any Hawaiian insect species, we have no quantitative indication of moisture-related limitations of insect distribution in the Hawaiian systems.

Biotic Aspects

Vegetational diversity

Temperature and moisture regimes determine the distribution of endemic plant species. Krajina (1963) described 14 biogeoclimatic zones, elaborating on the works of Rock (1913), Ripperton and Hosaka (1942), Fosberg (1961), and others, compiling ecological observations and studies of topographic, geological, climatic, and biotic factors. Five of these zones exist in the Manuka study area, reflecting a leeward forest pattern. At lower altitudes (300-470 m) open mixed xerophytic and mesophytic forest grades into closed mixed mesophytic and xerophytic forest (470-850 m) which in turn gradually passes into mesophytic marine tropical and subtropical forest (850-1470 m) and rather suddenly passes into open mixed mesophytic and xerophytic scrub forest (1470-1690 m) and finally to open xerophytic scrub (1690 m to subalpine and alpine elevations). The area has been largely characterized as a "dry transitional forest," based upon the vegetational community gradients, but the diversity of the communities is affected by differences in substrate, making the area far more complex.

Aerial photographs of the study area taken in 1962 show that the substrate varies in both age and basic composition. Unweathered 'a'a and cinderfalls may be found alongside sections of older, weathered substrates with good soil developement. Differential vegetation type is seen to correspond to differing substrata.

Results of a vegetation survey and ecological study conducted concurrently with the entomology collections of this study show that vegetational diversity changed with altitude. For example, at the 1690 m site, a plant species count tallied a maximum of 15 vascular plant species. At 1440 m, 52 vascular plant species were collected, and at 1150 m, 35 vascular plant species were encountered. At 875 m, 37 vascular plant species were tallied, and at 585 m, 39 vascular plant species were

counted at the main transect relevés. When the correlation coefficient r was computed for insect family diversity and plant species count, a strong correlation was seen ($r = 0.811$, $n = 10$). The relationship between the number of plant species and the number of insect families at identical plotsites reflects the correlation (Fig. 4).

Two major factors may be responsible for the relationship: trophic relationships between insects and plants, and the effect of spatial heterogeneity on species diversity.

The major relationship between insects and plants is trophic, and thus the ecology of the vegetation has a direct bearing on insect ecology. This would be most evident in stenophagous insects (i.e., insects with narrowly limited diets). Swezey (1954) compiled an annotated checklist of the insect faunas of Hawaiian forest plants, making note of stenophagous species. The percentage of stenophagous insects ranged from an 11% incidence of stenophagy (on Acacia koa), to a 72% incidence of stenophagy (on Pelea spp.). For the majority of endemic plant species, however, the incidence of stenophagy ranged between 30% and 45%, and the mean incidence of stenophagy in the Hawaiian herbivorous insects in 36.55%, a sizeable percentage.

The various Hawaiian plant species are host to a diverse number of insect species, ranging from eight known associated species on Osteomeles sp. to more than 128 known to feed on Acacia koa. Each plant species in the vegetational community could "contribute" its complex of associated insects to the total insect fauna. In the same manner, the absence of a plant species in a given area would mean that its stenophagous insect complement would be missing from the fauna. In our study area, the coleopteran families Bostrichidae, Cerambyciidae, and Carabidae were restricted to the 875 m plotsites and lower. The homopteran families Cicadellidae and Cixiidae likewise become extremely common below 875 m. Both families' predominance seem to be related to a change in vegetation below 940 m. Psychotria, a tree species in the family Rubiaceae becomes common in the canopy. Various dryland tree species such as Antidesma, Drypetes, and Diospyros make their appearance below 800 m and occur in their highest frequency just below 600 m. The increase in the number of tree species may explain the appearance of the coleopteran families, notable wood borers of various Hawaiian trees. The prevalence of the homopteran families may be related to the prevalence of Psychotria, from which both cixiids and cicadellids were collected in large numbers in day collections.

The predatory families Chrysopidae, Braconidae, and Bethylidae become prominent in the lower altitude plotsites, although the chrysopid lacewings and the braconid wasps were present at much lower numbers at higher plotsites. It is likely that either prey species became more numerous at lower altitudes, or that biomass of the prey population became greater. Both situations were seen to occur. The increase in predatory and parasitic families can be considered an indirect result of the increase in

plant species diversity. The more diverse the vegetational community, the greater is the potential for species packing in the consumer community and likewise in the entire trophic network.

In addition to trophic relationships, increased vegetational diversity results in an increased spatial heterogeneity. There is an increase in the complexity of the physical environment. For example, the higher abundance of Psychotria sp. in lower altitude plotsites means that there are differences in the trophic niche, habitat changes in the litter layer, unique resiance opportunities for day-inactive insect species, a new bark habitat for the psocopteran and orthopteran families, etc. In short, the more complex the physical environment becomes, the more complex the plant and animal communities supported, and the higher the species diversity. MacArthur (1965) suggested that between-habitat diversity is a major scheme in determining tropical species packing. For example, MacArthur and MacArthur (1961) determined that the extent of foliage stratification in a forest community was more important than the species diversity of the vegetational community alone in affecting the faunal diversity. In the Manuka study, foliage stratification increased with lower altitude, as conditions improved for tree species. At the 1150 m plotsites, the canopy of Metrosideros was non-interlocking and rose to about 6 m. Forest conditions developed by 875 m, however, with densely interlocking canopies of Metrosideros and Psychotria, reaching crowns at 25 m. The substantially tall canopy created adequate room for a well-developed middle-story of Cibotium tree ferns, Myrsine lessertiana, and Vaccinium calycinum, and an understory of ferns and small vascular plants. In the 585 m plotsites, species diversity was even higher, and the complexity of foliage stratification was very well developed. It is not surprising that the increase in species diversity and foliage stratification downslope in the study area is paralleled by a correspondant increase in the diversity of the insect community.

Combination of factors

All of the factors discussed this far cannot be realistically considered independently. The combination of environmental aspects and biotic factors is a dynamic process, the synthesis of which is the final characteristics of insect distribution we have observed. For example, moisture characteristics probably determined the basic vegetational diversity at 875 m; however, the presence of vegetation can create microclimates in which moisture and temperature conditions are quite different from adjacent, barren areas at the same altitude. As a result, the increase in the complexity of the environment created by microclimates would allow for a higher potential in species diversity. What will be discussed next is an example of the resultant effect of a combination of environmental and biotic factors: the "hump" phenomenon at 1440 m.

The "hump" phenomenon

The exceptionally high diversity of the 1440 m plotsite collection can be considered in terms of the interaction of several factors which exist at that elevation. It can be seen that perhaps three aspects unique to the 1440 m plotsites could contribute to the "hump" phenomenon: moisture conditions, vegetational diversity, and kipuka effects.

An inversion layer fog belt which exists from 1080 to 1860 m creates a high humidity situation without heavy precipitation. It has been suggested that for some species of Hawaiian insects, the physical effect of rain showers may restrict their presence in zones of precipitation (Gagné 1976). In addition, high air moisture creates favorable conditions for the growth of fungus, and results in suitable habitats for detritivorous and fungivorous insects, which constitute a considerable percentage of Hawaiian forest insect communities (Gagné 1976). In our study, the dipteran families Dolichopodidae and Cecidomyiidae were restricted between 1160 and 1500 m.

The importance of fog drip as a major mode of water uptake in the Hawaiian forest has been documented (Juvick & Perreira 1973). In the Manuka study, we found that not only is there a more luxuriant vegetational situation created, but vegetational diversity is highest in the fog zone.

In addition, the 1440 m plotsite sampling was conducted in a kipuka of moderate size. Generally, a kipuka, or regional unconformity (Pukui & Elbert 1971) is a section of vegetation surrounded by the relative infertility of fresher lava substrate. In many cases, the change in species diversity and community structure of vegetation moving from barren lava to within the lush kipuka environment promises to show consistent patterns, allowing the kipuka concept to be defined ecologically. Yoshinaga and Anderson (1977, unpub. ms.) studied the kipuka systems of the Manuka-Kapu'a area and found that because of the insular character of kipukas, their habitat differs from continuous stands of old substrata as well as from that of the surrounding fresh lava. Compared to the open lava, the more weathered kipuka substrate has better moisture-holding capacity, more available nutrients, and better rooting opportunities. The more closed canopy offers shelter for species unable to tolerate the hot, dry open environment of the surrounding undecomposed lava. Litter may collect more effectively than in the open. Along the perimeter of a kipuka exists a strip of edge habitat, which can support species which might be unable to grow in closed forest. Just outside the kipuka is a boundary habitat, where the harsh environment of the lava flow may be somewhat ameliorated by the effects of the kipuka such as shade, fog drip, and leaf litter. The plant species list for soil kipukas in our study area was similiar to a combined species list for open lava and continuous stand vegetation on soil. Thus, in the kipuka situation, a combination of high plant species complement, higher potential

vegetational situation, and habitats unavailable to both surrounding lava and continuous stand forest, can be considered as factors contributing to an increased insect diversity.

In summary, Figure 3 illustrates the diversity of habitat and climatic conditions which contribute to the "hump" phenomenon at 1440 m: fog conditions, general vegetational diversity, and kipuka effects. In addition, Figure 3 demonstrates gradients in moisture and vegetation that are pertinent to the general relationship of altitude and insect diversity uncovered in this study.

CONCLUSION

In the Manuka-Kapu'a study, nocturnal insect diversity at the family level increased as altitude decreased, with the exception of a disproportionately high diversity at the 1440 m elevation. The general altitude effect was attributed to the interrelation of three major factors: temperature, moisture, and vegetational diversity. Although it is clear that temperature and moisture conditions contributed indirectly to insect distribution by determining vegetational diversity and structure, it is not known what direct limiting effect thay have on the Hawaiian insect species. It is recommended that physiological studies be conducted, focusing on the tolerances of Hawaiian species to a wide range of temperature and moisture conditions, determining survivorship thresholds and optimum ranges. The information from such studies could be used to test whether temperature and moisture limitation is a mechanism directly determining the distribution of Hawaiian insects in field studies.

The exceptionally high diversity at 1440 m was attributed to three major factors not present at other plotsite locations: fog belt conditions, unique vegetational species complement, and the effects of kipukas.

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TABLE 1. Number of families encountered in night collections of isoaltitudinal plotsites, Manuka Forest Reserve, South Kona, Hawai'i (A = main transect; B = auxilliary transect; K = Kapu'a transect).

Transect Plotsite	Total Families	$\bar{X}$ by Altitude	Total by 8:30 P.M.	$\bar{X}$ by Altitude
1690A	10	10.00	5	5.00
1440A	18		15	
1440B	13	15.67	10	12.67
1440K	16		13	
1150A	14		10	
1150B	13	14.67	11	10.33
1150K	17		10	
875A	15		11	
875B	16	17.67	13	14.00
875K	22		18	
585A	24	21.50	18	18.00
585B	19		18	

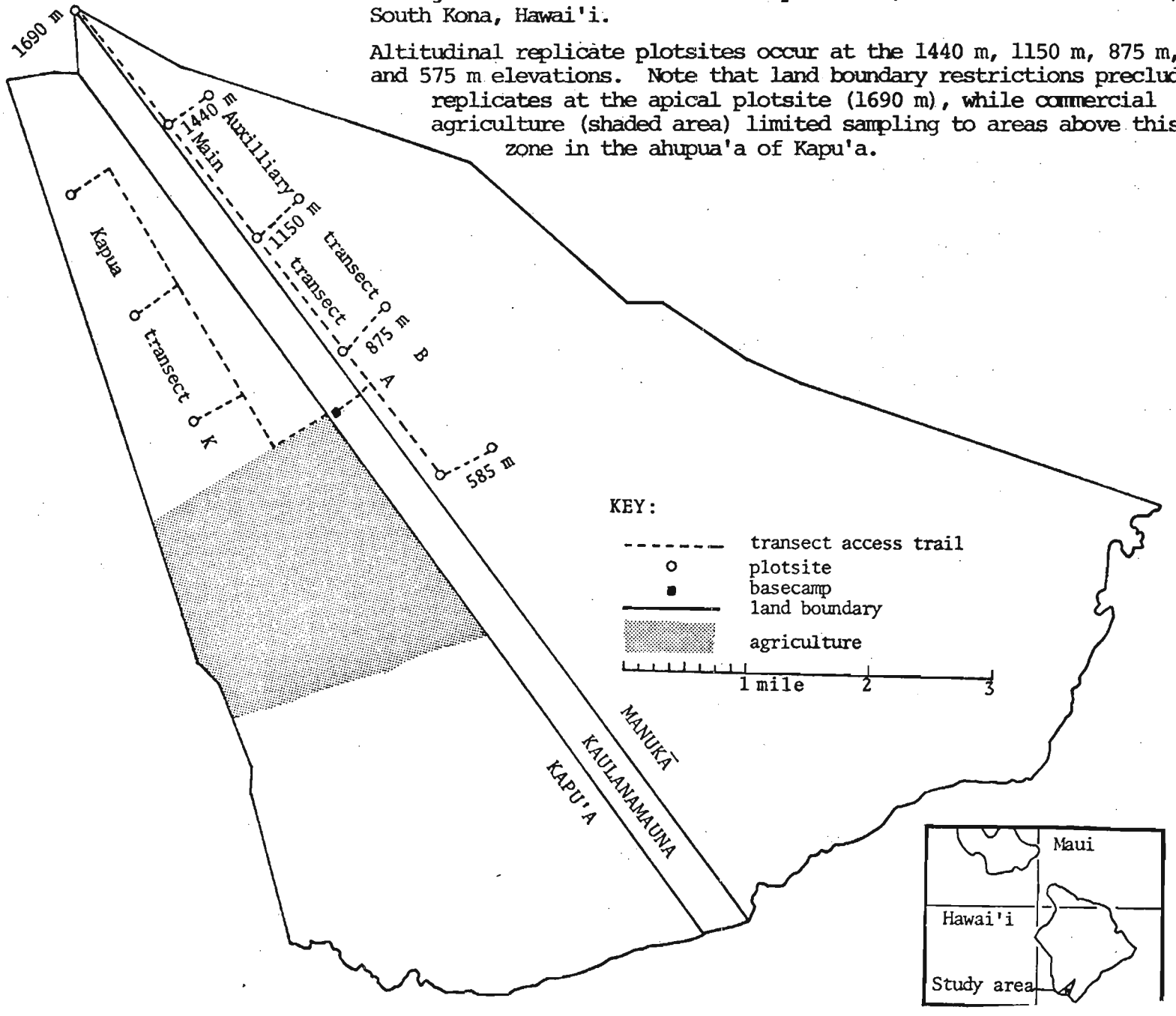

FIGURE 1. Arrangement of transect lines and plotsites, Manukā Forest Reserve, South Kona, Hawai'i.

Altitudinal replicate plotsites occur at the 1440 m, 1150 m, 875 m, and 575 m elevations. Note that land boundary restrictions preclude replicates at the apical plotsite (1690 m), while commercial agriculture (shaded area) limited sampling to areas above this zone in the ahupua'a of Kapu'a.

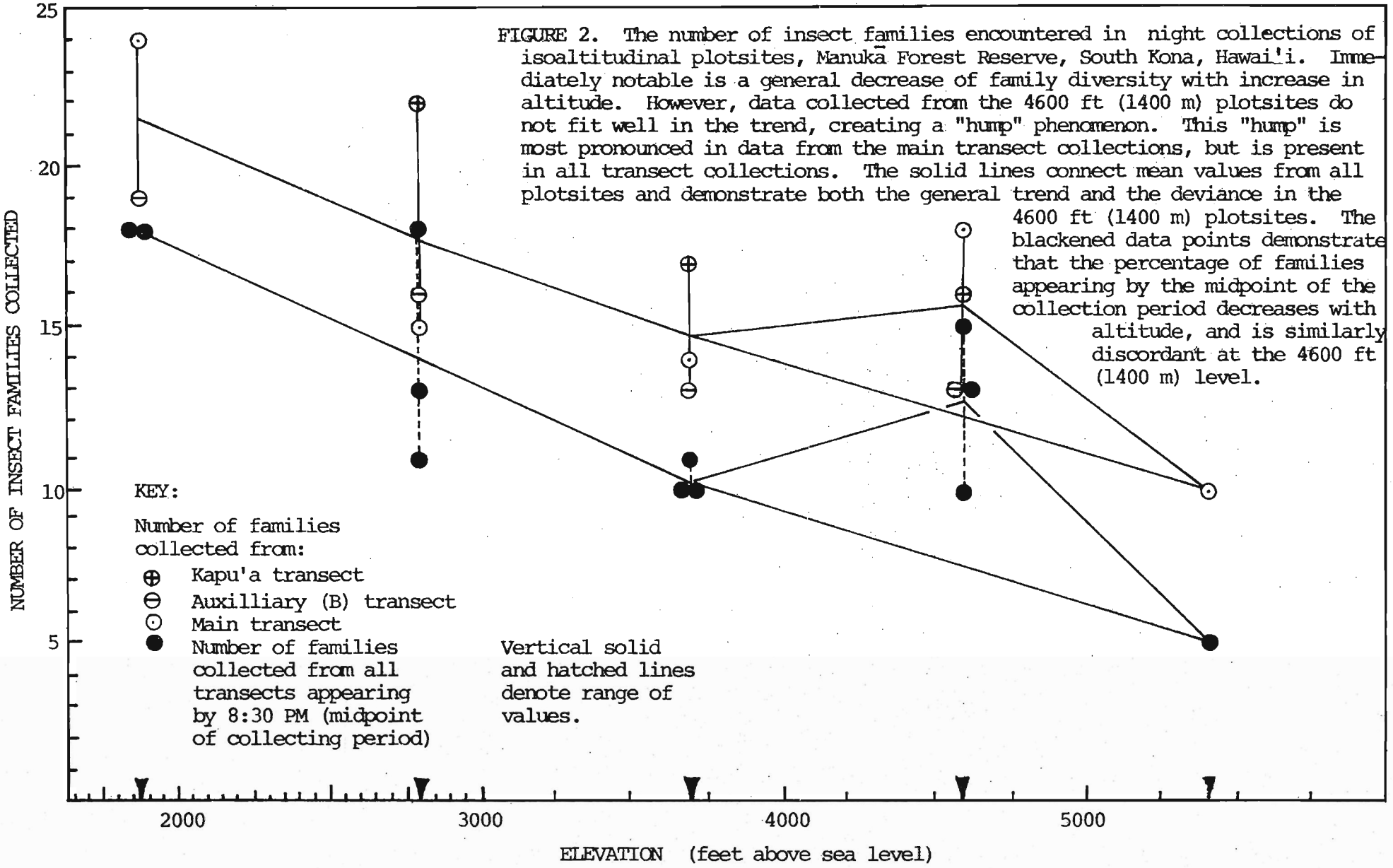

FIGURE 2. The number of insect families encountered in night collections of isoaltitudinal plotsites, Manukā Forest Reserve, South Kona, Hawai'i. Immediately notable is a general decrease of family diversity with increase in altitude. However, data collected from the 4600 ft (1400 m) plotsites do not fit well in the trend, creating a "hump" phenomenon. This "hump" is most pronounced in data from the main transect collections, but is present in all transect collections. The solid lines connect mean values from all plotsites and demonstrate both the general trend and the deviance in the 4600 ft (1400 m) plotsites. The blackened data points demonstrate that the percentage of families appearing by the midpoint of the collection period decreases with altitude, and is similarly discordant at the 4600 ft (1400 m) level.

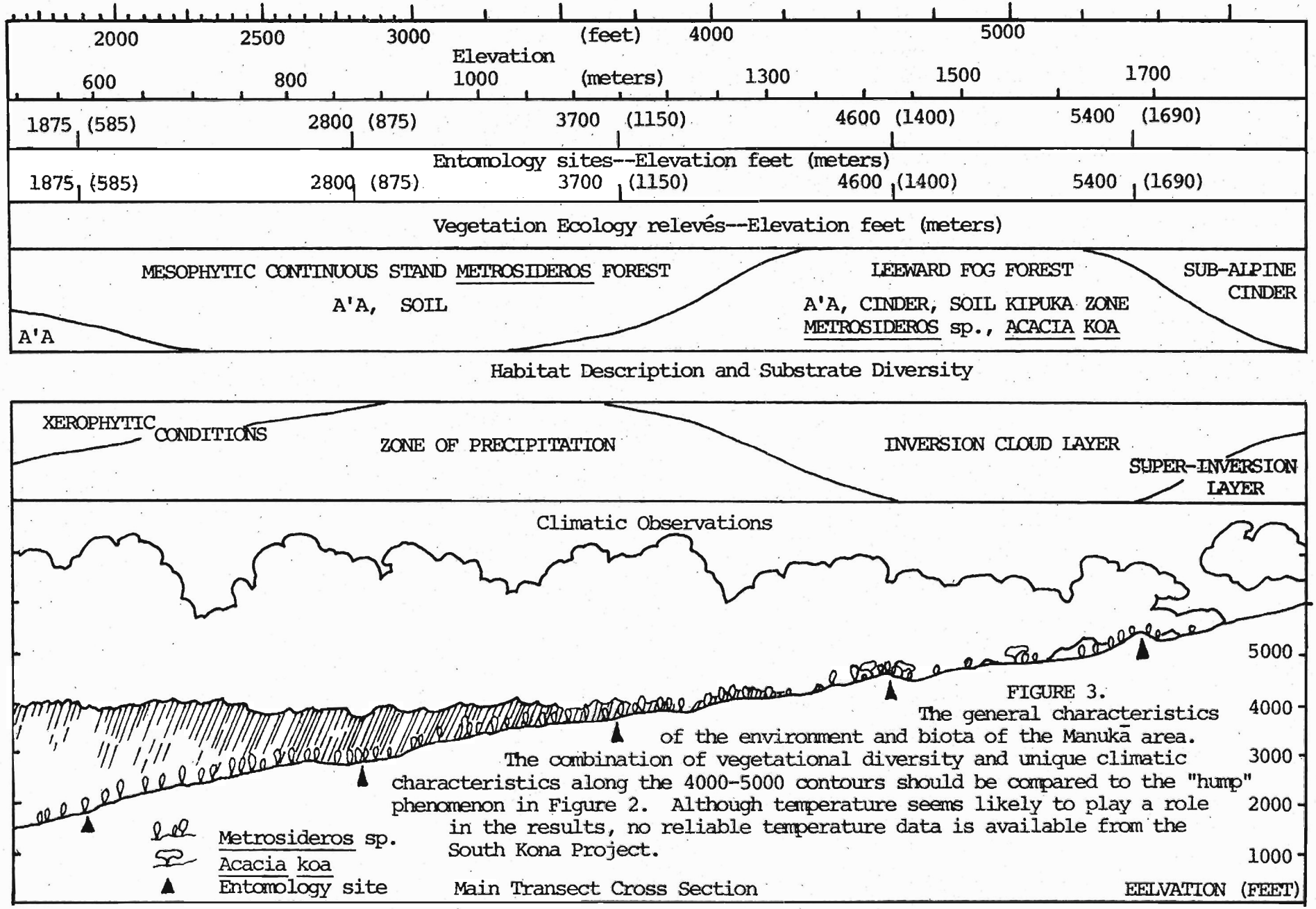

FIGURE 3.
The general characteristics of the environment and biota of the Manukā area.

The combination of vegetational diversity and unique climatic characteristics along the 4000-5000 contours should be compared to the "hump" phenomenon in Figure 2. Although temperature seems likely to play a role in the results, no reliable temperature data is available from the South Kona Project.

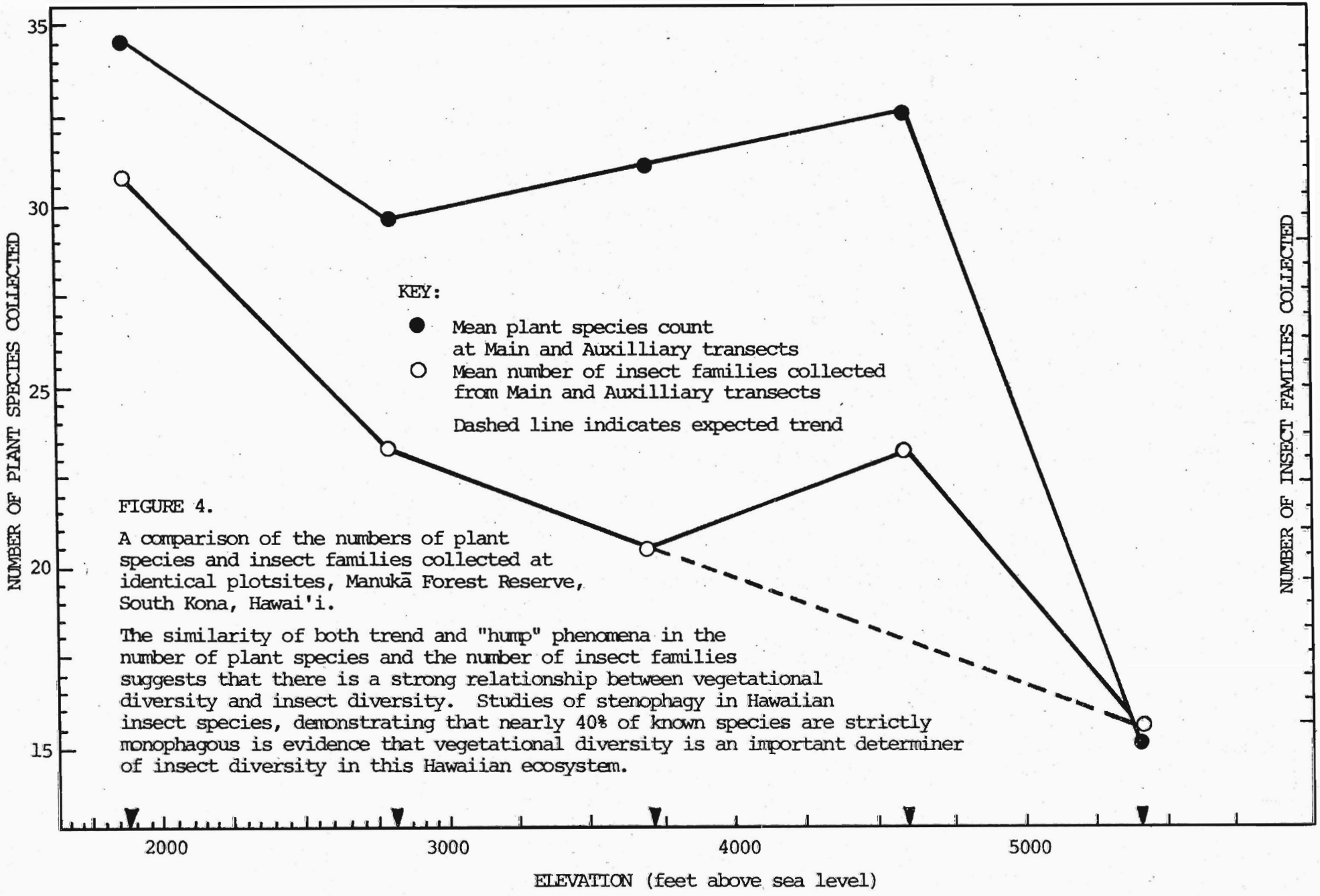

FIGURE 4.

A comparison of the numbers of plant species and insect families collected at identical plotsites, Manukā Forest Reserve, South Kona, Hawai'i.

The similarity of both trend and "hump" phenomena in the number of plant species and the number of insect families suggests that there is a strong relationship between vegetational diversity and insect diversity. Studies of stenophagy in Hawaiian insect species, demonstrating that nearly 40% of known species are strictly monophagous is evidence that vegetational diversity is an important determiner of insect diversity in this Hawaiian ecosystem.